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RESEARCHES ON THE STRUCTURE AND FUNCTION OF THE MAMMALIAN HEART. BY A. F. STANLEY KENT, M.A.

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RESEARCHES ON THE STRUCTURE AND FUNCTION  
OF THE MAMMALIAN HEART. BY A. F. STANLEY  
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(Pl. XII.)

*Object of the Research.*

THE views held by physiologists concerning the mode of action of the Mammalian heart have been based upon the assumption put forward in various books and papers dealing with the subject, that there exists a profound difference between the hearts of the lower vertebrates on the one hand and the hearts of mammals on the other. And this difference is supposed to be of such a kind as to entirely prevent a similar explanation of certain cardiac phenomena being accepted in the two cases. Briefly the phenomena in question are concerned with the passage of the wave of contraction over the auriculo-ventricular groove, an explanation being required of the mode in which an auricular contraction is able on arriving at the groove to initiate a contraction of the ventricle. In cold-blooded animals there is no difficulty in finding a satisfactory explanation, inasmuch as it is well known that the muscular tissue constituting the various chambers of the heart is in these animals perfectly continuous from the sinus venosus through the auricles into the ventricle, and the explanation of the passage of a wave of contraction over the various chambers is upon exactly the same footing as the explanation of the passage of a wave of contraction along any other continuous stretch of muscular tissue.

With the mammal, however, the case has up to the present appeared to be different, inasmuch as no such continuity has been known to exist, but on the contrary a distinct break has always been described as existing between the muscular fibres of auricle and ventricle. The existence of this break has rendered inadmissible any explanation which depends upon muscular conduction and has placed the phenomenon in the mammal upon an entirely different footing to

that which it occupies in the frog. Moreover it is extremely difficult to formulate any theory that shall adequately explain all the observed phenomena, and whilst much ingenuity has been exercised in attempting such explanation, any exhaustive examination of the relations of structures actually existing at the auriculo-ventricular junction appears to have been neglected.

### *Historical.*

It has long been known that the various chambers of the heart in the lower vertebrates are made up of a mass of muscular fibres intermediate in structure between the ordinary striated fibres of the voluntary muscles and the non-striped muscle which is found in many of the viscera<sup>1</sup>. It is further well known that the fibres of which the various chambers are built up whilst having many characters in common, yet differ to a certain extent, and a regular series can be recognised, the fibres taken from the auricles presenting characters intermediate between those of fibres taken from the sinus on the one hand and the ventricle on the other. The general type of these fibres is represented by a long, slender, nucleated, spindle-shaped cell in the frog, and these cells closely resemble non-striped muscular fibres, save that they are somewhat larger and that their substance is transversely striated, the striation being due to alternate dim and bright bands. Like the plain muscular fibre, the cardiac muscular fibre has no distinct sarcolemma. The fibres of the auricle are more usually branched than those found in the ventricle, and many become so extensively branched as to be almost stellate<sup>2</sup>. Amongst the striated fibres are found plain muscular fibres and these increase in relative number along the roots of the great veins, until nothing but plain muscle is to be found.

In the bulbus arteriosus are found fusiform fibres which close to the ventricle are striated, but at a certain distance from the ventricle pass into fusiform fibres having the characteristics of plain muscle.

In the case of the mammalian heart, both the auricles and ventricles are formed of bundles of muscular tissue, bound together by connective tissue and arranged in a very complex system of sheets. The histological unit of these muscular bundles is a prismatic nucleated cell, provided usually with one or more broad lateral processes. No definite sarcolemma is present; the protoplasm of the cell is transversely striated, the striations being due as in skeletal muscle to

<sup>1</sup> MacWilliam. *This Journal*, Vol. ix. p. 186.

<sup>2</sup> Foster. *Text-book of Physiology*.



alternate dim and bright bands. These cells are joined at each end by cement substance to other similar cells, and by the junction of the lateral processes of neighbouring cells a network is formed. Networks of a higher order are formed by the weaving together of these fibres and bundles of fibres by means of connective tissue in which run vessels of various sizes. The sheets or bundles composed of such networks are arranged in a complex manner both in auricle and ventricle<sup>1</sup>. Plain muscular fibres are frequently found under the endocardium and similar fibres are said to spread from the endocardium into the auriculo-ventricular valves.

So far then as the histological unit is concerned, the differences between the mammalian and non-mammalian heart are comparatively slight, both being composed of more or less obscurely striated, nucleated, granular cells of elongated form, woven into bundles and arranged as more or less complicated networks which form the walls of the cardiac chambers. In both also are found plain non-striated muscle cells, and in both connective tissue is found binding the bundles together. It is however when the arrangement of these bundles is studied that important differences are seen, for whilst in the frog's ventricle the fibres are woven into an intricate spongework devoid of blood vessels, in the mammal's ventricle the sheets of muscle are arranged in a very complex but perfectly definite series of layers, these layers being continuous one with another at the apex, and, according to Pettigrew, at the base also. He says, "Unlike the generality of voluntary muscles, however, the fibres of the ventricles, as a rule, have neither origin nor insertion, i.e. they are continuous alike at the apex of the ventricles and at the base<sup>2</sup>." That this is not always the case, however, will be evident from some facts that I shall have to state farther on.

Besides this difference in general arrangement, a more special and functionally far more important difference is said to exist in the relation of the muscular fibres of the auricle to those of the ventricle. In the case of the frog and in non-mammalian animals generally, there exists between the different chambers a complete muscular continuity, bundles of fibres running from the sinus to the auricles and from auricles to ventricle<sup>3</sup>.

In the mammal a very different arrangement is described. And a writer who perhaps has devoted more attention to the arrangement of

<sup>1</sup> Foster. *loc. cit.*

<sup>2</sup> *Physiology of the Circulation*, p. 192.

<sup>3</sup> MacWilliam. *loc. cit.*

the muscular fibres of the heart than any other, states emphatically that the auricles are anatomically distinct from the ventricles, and he states in proof of this, that in boiled hearts the auricles and ventricles may be separated from each other without rupturing a single fibre<sup>1</sup>. The proof appears to me to be far from conclusive, for in addition to the difficulty of distinguishing the presence of isolated muscle fibres with absolute certainty even under ordinary circumstances, it is probable that in the process of boiling, both the muscular fibres would become less easily recognisable and the swelling up of the fibrous tissue would mask, and perhaps even rupture, any slender fibres that might exist.

More recently another writer has stated that "in the mammalian heart the structural connection of the great veins with the auricles is essentially similar to what obtains in cold-blooded animals, inasmuch as there is muscular continuity between the venous and auricular walls; the problem as to the mode of propagation (of the wave of contraction) may be said to stand on the same footing as in the lower vertebrates. But the question as to how the contraction is propagated from auricles to ventricles stands on an entirely different basis, inasmuch as the structural relations of these parts to one another are entirely different. Instead of complete muscular continuity throughout the heart, there occurs in the mammalian heart a distinct break—a distinct interval—between the muscle of the auricles and the muscle of the ventricles. The auricular fibres and the ventricular fibres belong to systems of their own, and are separated by a considerable amount of connective tissue at the auriculo-ventricular junction. The part where the auricular and the ventricular muscular fibres are most closely approximated, is at the base of the auriculo-ventricular valves, but even in that situation there is a distinct want of continuity, a well-marked separation between the auricular and ventricular systems<sup>2</sup>."

Similar statements are also to be found in the text-books<sup>3</sup>. And this view of the relation of auricle to ventricle must render inapplicable to the mammalian heart the hypothesis which perhaps seems to best

<sup>1</sup> Pettigrew. *loc. cit.*

<sup>2</sup> MacWilliam. *This Journal*, ix. 187.

<sup>3</sup> Gray's *Anatomy*, Edition 11, p. 841. Ellis, *Demonstrations of Anatomy*. Landois, *Text-book of Human Physiology*, translated by W. Stirling.

explain the passage of the wave of contraction over the auriculo-ventricular groove in the hearts of cold-blooded animals.

It has been urged by Gaskell<sup>1</sup> that in the heart of the tortoise the ventricle contracts in due sequence with the auricle because a wave of contraction passes along the auricular muscle and induces a ventricular contraction when it reaches the auriculo-ventricular groove, that is to say, the contraction is propagated over the heart by muscular conduction; and although other observers are inclined to think that in consequence of the complex way in which the finest nerve fibres ramify among the muscular fibres, it is impossible to exclude the possibility of an important conducting function being discharged by these nerve fibres, yet the phenomena observed agree so closely with those seen during the passage of the wave of contraction over any other continuous muscle that it is impossible to conceive of the muscular fibres at the groove as being entirely passive in the matter and the nerves as being all important. Moreover there is evidence to show that at all events the larger intracardiac nerves and the ganglia are not at all necessary for the efficient propagation of the contraction. But in the mammal any explanation based upon muscular conduction is excluded, and we are thrown back upon some other explanation. Hypotheses have been put forward depending upon electrical, mechanical, and nervous causes, and whilst the electrical and mechanical explanations are often ingenious, it is probable that most weight has been given to explanations depending upon nervous agency. In the early days of physiology before the continuity of the cardiac muscular fibres was fully appreciated, arguments were given and experiments made to show that the contraction passed from fibre to fibre in consequence of a mechanical stimulus given by the contraction of one fibre to the nerve fibres supplying the muscle fibre next in order. And to explain the transmission of the wave over the auriculo-ventricular groove, it would have been necessary merely to suppose a slight lengthening of these connecting nerve fibres to take place. But since it soon became evident that under certain conditions the different parts of the heart were able to contract singly and separately, it was seen that the conception of a peristaltic wave did not quite meet the requirements of the case, and Schiff concluded that the loss of time between the auricular and ventricular contractions was due to a delay in the nervous impulse reaching the ventricle, although it was started from the venous

<sup>1</sup> This *Journal*, iv. 64.



sinus at the same time as the impulse for the auricle; that is to say, that by some means the impulse travelling from the venous sinus towards the ventricle is blocked and in consequence takes effect at a later moment than the impulse, simultaneously generated, which passes to the auricle.

Lately a modification of this view has been held, and the co-ordination of the auricular and ventricular contractions has been regarded as being largely dependent upon the action of nerve cells in the substance of the heart.

But as above stated, there is evidence to show that the ganglia are non-essential.

And the evidence in favour of a mechanical or electrical explanation of the propagation is equally unsatisfactory. For in the case of that hypothesis which seeks to find in the increase of ventricular blood pressure consequent upon the auricular contraction, an efficient cause for the ventricular contraction, we are met by the difficulty that even in an empty heart the same sequence occurs. Moreover Wooldridge and Tigerstedt have made experiments in which, after physiologically disconnecting the ventricles from the auricles (by crushing or cutting the auriculo-ventricular junction) without materially interfering with the flow of blood through the cavities of the heart, they found that the ventricles exhibited a rhythmic action quite independent of the auricular action; a ventricular beat did not follow each auricular beat as in the normal heart. And although it is possible that the excitability of the ventricular tissue may have been modified by the operative interference, yet it is hardly probable that the whole result was due to such modification, inasmuch as in the intact heart the ventricular sequence often "persists with complete regularity even after the ventricles have suffered a very decided diminution of their irritability."

It has been suggested that the electrical variation of the auricle might act as a stimulus to the ventricular muscle, but in the first place the auricular current is very weak, and in the second, the sequence is not interfered with when precautions are taken to short circuit the current by immersing the heart in mercury.

It has also been suggested that the ventricular sequence may be due to the mechanical excitation of the ventricular fibres by the contraction of the auricle—or rather by the contraction of the muscular fibres of the auriculo-ventricular valves—pulling upon the chordæ tendineæ.

MacWilliam however, has made experiments in which the chordæ tendineæ were severed by making a section across the upper part of the

ventricles so as to leave the upper third of the ventricles in connection with the auricles. In a heart thus operated upon, in which the chordæ were completely divided, the sequence continued unimpaired for a considerable time, and in addition to this, artificially excited contractions of the auricles could be propagated to the ventricles and similarly artificially excited contractions of the ventricles could be propagated to the auricles.

From what has been said it will be evident that it is impossible to account for the normal sequence of ventricular upon auricular beat upon purely physical grounds, but I do not draw from this the conclusion that the propagation of the contraction from auricles to ventricles is effected through the nerves that pass between these parts, but rather that the knowledge that we have up to the present time possessed, has been insufficient to enable us to explain aright such propagation.

Accordingly, I have recently made experiments with the object of increasing our knowledge of the structure of the heart, and have described in the following pages the results of such experiments and the conclusions respecting the passage of the wave of contraction over the auriculo-ventricular groove which these results have led me to adopt.

#### RESULTS OF EXPERIMENTS.

The experiments have been made upon Monkeys, Dogs, Cats, Guinea-pigs, Hedgehogs, Rabbits, and Rats, and in almost all cases animals of various ages have been used.

#### *Histological.*

In commencing an inquiry of this sort, it is natural to look for help to the embryological development of the organ in question.

Comparing then the development of the heart in Amphibia and Mammalia, it is seen that in the former the heart originates as a tubular cavity in the splanchnic mesoblast, the walls of the cavity being formed of two layers, an outer thicker layer, which gives rise to the muscular wall and peritoneal coverings of the heart, and an inner lamina which is the epithelial lining of the heart. In the mammals, in which the heart is formed before the conversion of the throat into a closed tube, the heart arises as two independent tubes which eventually coalesce into an unpaired structure. By becoming twisted upon itself

and divided by constrictions and septa, the muscular tube becomes converted into the multilocular heart of the adult.

This being the course of development, it would appear that by taking a sufficiently early stage it should be possible to obtain a condition in the mammal comparable to the condition permanent in the frog,—a condition that is, in which the primitive continuity of the outer thicker wall of the tube should be preserved as a continuity of muscular fibres throughout the heart, a condition earlier than that in which the separation between the auricular and ventricular systems of muscular fibres (supposing such to occur) takes place. And for the purpose of seeking such a condition it is desirable that some animal be taken in which at birth the foetus is in a comparatively rudimentary condition. Such an instance occurs in the case of the rat, the young of which animal are born in an early stage of development, and accordingly my earliest observations were made upon newly-born rats. And it soon became manifest that in this animal at any rate a condition of things obtains which is strictly comparable to that found in the frog, for instead of the bundles of muscular fibres belonging to the auricle being sharply marked off from those belonging to the ventricle, the very reverse is the case, the fibres being quite continuous and streaming through at the junction of auricles and ventricles as a strand of considerable size.

Fig. 1, Plate XII., represents part of a coronal section of the heart of a newly-born rat, the point of junction of the auricle and ventricle having been photographed. It is seen here that the cells forming the mass of the ventricular wall are somewhat different from the usual form of cardiac muscular fibres, being more fusiform and having more sharply tapering ends. The nuclei also have a more or less pronounced fusiform outline and strongly resemble the nuclei of non-striped muscle cells. At the upper part of the ventricle and in the angle formed by the auricular wall the muscular fibres of the ventricle are seen to have a direction somewhat different to that taken by the auricular fibres, but at about the centre of the isthmus the auricular fibres are seen to sweep freely down into the substance of the ventricular wall and other fibres are to be observed coursing from the auricle into the basal part of the valve. At this stage therefore it would appear that a muscular continuity exists between the auricle and ventricle, and also between the auricle and base of the auriculo-ventricular valve. Of this last I shall speak later.

Having then established such a muscular continuity between auricles and ventricles in the case of rats newly born, it remained to determine—



(i) whether this continuity became obliterated during growth and, in the case of this being established, (ii) the exact time at which such obliteration occurred. And for this purpose a series of animals was taken, of ages varying from two days up to maturity, and sections were prepared, for the most part as complete series right through the heart, the small size of the organ in the younger stages allowing this to be done with comparative ease.

The result of a careful study of these series has been to convince me that although a considerable development of connective tissue may take place in the region of the auriculo-ventricular groove, yet even in the adult animal a strongly marked band of muscular tissue remains and preserves the integrity of the muscular connection between the two chambers of the heart. And that this connecting sheet of muscle extends over a considerable distance is proved by the fact that it is plainly visible in a large number of sections in any one series, and moreover it is met with over a considerable area of the auriculo-ventricular groove; thus, it may be mentioned that frequently in a single coronal section the connection may be seen between the outer (left) wall of the left ventricle and the left auricle, between the septum ventriculorum and the auricle, and between the right wall of the right ventricle and the right auricle.

In the case of the junction between the septum ventriculorum and the auricle the fibrous tissue of the base of the valve penetrates a comparatively short way into the muscle, and in the deeper parts the fibres sweep uninterruptedly through from auricle to ventricle. The same state of things may be proved to exist where the right ventricle becomes continuous with the right auricle.

In the case of other animals the conditions appear to be somewhat similar, though in few animals have I found the foetal condition so well preserved in the adult form. In the young rabbit of two days old for example, the auricular fibres are seen sweeping down to the outer side of the fibrous ring and becoming continuous with bundles belonging to the ventricular system. The connection also exists on the right side of the heart between the right auricle and ventricle, and also in the septum to the right side of the ring bearing the mitral valve. The connective tissue forming the roots of the fibrous ring spreads out in a fan-shaped mass from the base of the valve, where it is very much condensed and forms a firm support for the segments of the valve. It appears to me that this condensation of fibrous tissue is due to an increase in the amount of connective tissue normally present



between the muscular bundles, and that its purpose is to afford a fixed point for the attachment of the auriculo-ventricular valves. And here it may be stated that Balfour is in error when he describes the valves as having no muscular connection with the walls of the heart. He says:—"In the primitive state the ventricular walls have throughout a spongy character; and the auriculo-ventricular valves are simple membranous projections like the auriculo-ventricular valves of Fishes. Soon, however, the spongy muscular tissue of both the ventricular and auricular walls, which at first pass uninterruptedly the one into the other, grows into the bases of the valves, which thus become in the main muscular projections of the walls of the heart. As the wall of the ventricle thickens, the muscular trabeculæ, connected at one end with the valves, remain at the other end united with the ventricular wall, and form special bands passing between the two. The valves on the other hand lose their muscular attachment to the auricular walls."

It is quite possible that the above description may be correct for certain animals, but it is undoubtedly the case in many of the animals that I have already examined that the auriculo-ventricular valve retains its connection with the muscular system of the auricle, a well-marked bundle of muscle fibre often running from the auricle and penetrating the upper part of the valve for a considerable distance. The muscular bundles of the ventricle, on the other hand, appear to stop short when they reach the dense connective tissue forming the root of the valve, and the fibrous stroma of the under surface of the valve appears to be largely reinforced by a special development of connective tissue lying immediately beneath the endocardium.

It has been said that the muscular continuity between auricles and ventricles persists in the adult hearts of all the animals that have yet been examined, but it must be understood that very considerable differences exist in the perfection of this connection, or rather in the number of fibres running from the one chamber to the other, and also in the exact mode in which the connection is brought about. In the monkey, for instance, it is far more difficult to find a point at which a considerable number of fibres cross the groove than is the case in the rat, and in addition to this almost every animal examined, whilst agreeing with the general type in possessing a more perfect muscular connection in the early than in later stages, yet presents, in the adult, certain peculiarities in the structure and distribution of the connecting fibres.

In the Guinea-pig, for example, we find that the fibrous ring is

more developed than was the case in the rat, but just as in that animal a portion of the muscle of the auricle sweeps through uninterruptedly into the ventricle, the principal difference between the two cases being in the number of fibres forming the connection. And in the Hedgehog the arrangement is very similar.

It is in the Monkey, however, that we find the most marked departure from the foetal type of arrangement. In this animal the fibrous ring has attained a very perfect development and it is only here and there that places can be found to show the passage of muscular fibres across the groove. Such places nevertheless can always be found by a careful search, and I have no hesitation in affirming that a connection always exists. In many preparations I have traced the fibres the whole distance and assured myself that the connection is perfect.

But in addition to this comparatively simple mode of connection, we have in the Monkey remarkably well developed a second and far more complicated system of communicating fibres, indications of whose presence we may find lower down in the scale, inasmuch as they are recognisable even in the rat. For upon looking carefully at a favourable preparation of the heart of this animal it will be noticed that lying on the borderland between the undoubted muscle on the one hand and the connective tissue on the other, and even penetrating the latter sometimes to a considerable distance there may be distinguished cells which whilst certainly not belonging to the connective tissue, yet differ very markedly from the muscle fibres in the immediate neighbourhood. Briefly, these cells are usually spindle shaped, nucleated, granular and often transversely striated and are obviously a form of muscular tissue intermediate between ordinary cardiac tissue and plain or non-striated muscle. Sometimes even in the rat these cells are seen to present indications of branching and sometimes extend almost completely through the fibrous ring.

In the Monkey these fibres are far more perfectly developed and present a complete network permeating the fibrous connective tissue and extending through from auricle to ventricle. Not only are these fibres present in the connective tissue but the normal cardiac muscle on approaching the groove appears to split up into similar fibres and becomes connected with the network of cells previously mentioned, and in this way a second system of communicating fibres is established between auricle and ventricle (see figures, Plate XII.).

The mode of connection of the typical cardiac tissue with this





FIG. 1.

Sketch of the section of heart of adult Rat, showing junction of right auricle and ventricle. In the upper part of the figure is the outer-wall of the right auricle, below and to the right is the wall of the right ventricle, and below and more to the left is the mass of tissue from which springs the auriculo-ventricular valve. The cavity of the heart is to the left. It is seen that a band of muscle runs almost completely round from auricle to ventricle, *bordering closely upon the cavity of the heart*. At the lower part this band becomes continuous with a network of branched muscle cells lying in the interval between auricle and ventricle. These branched fibres become continuous on the right with the muscular tissue of the ventricle.

system of branching cells appears to be slightly different in the auricle and ventricle. In the auricle comparatively large bundles of fibres suddenly split up into a number of radiating branches and often present the appearance of a more or less stellate mass of fibres lying at the edge of the fibrous ring. The branches become further divided up and are continuous with elongated cells forming part of the network. In the case of the ventricle on the other hand as the bundles approach the fibrous tissue the direction of their fibres becomes more and more parallel, and they finally reach the "ring" as long leashes of very fine fibres which become more slender as they penetrate the fibrous tissue and finally come to consist of a few fibres only. Meanwhile these fibres have been undergoing modification from the ordinary type of cardiac muscle fibre and have taken on the form of elongated and very slender fibres with finely tapering ends. The transverse striation is well seen. The muscle is continued through the fibrous tissue for some distance as bundles consisting of 3-6 such fibres and then the number of fibres becomes still farther reduced to 2-3. These sometimes become branched, separate from one another, and are continued as single fibres which run unaltered for some distance, then become branched again and anastomose with other similar fibres to form a fairly close network. The fibres are sometimes reduced to mere threads, bulging at every nucleus, but even in the thinnest parts the transverse striation is plainly visible. Occasionally at the point from which several branches start a nucleus lies imbedded in a mass of protoplasm of more or less quadrilateral shape. In other cases the protoplasm surrounding the nucleus may be fusiform, and in others again scarcely any protoplasm may be visible round the nucleus.

The whole system of branching fibres appears to form a network continuous on the one hand with the muscle of the auricle and on the other with the muscle of the ventricle.

It would appear then that the fact of two masses of muscle being joined together by fibrous tissue is in itself no argument against the muscular continuity of such masses, the fibrous nature of the intervening tissue by no means excluding the possibility of muscular fibres running through it and preserving the muscular connection.

And in the Mammalian heart such a connection appears to exist.



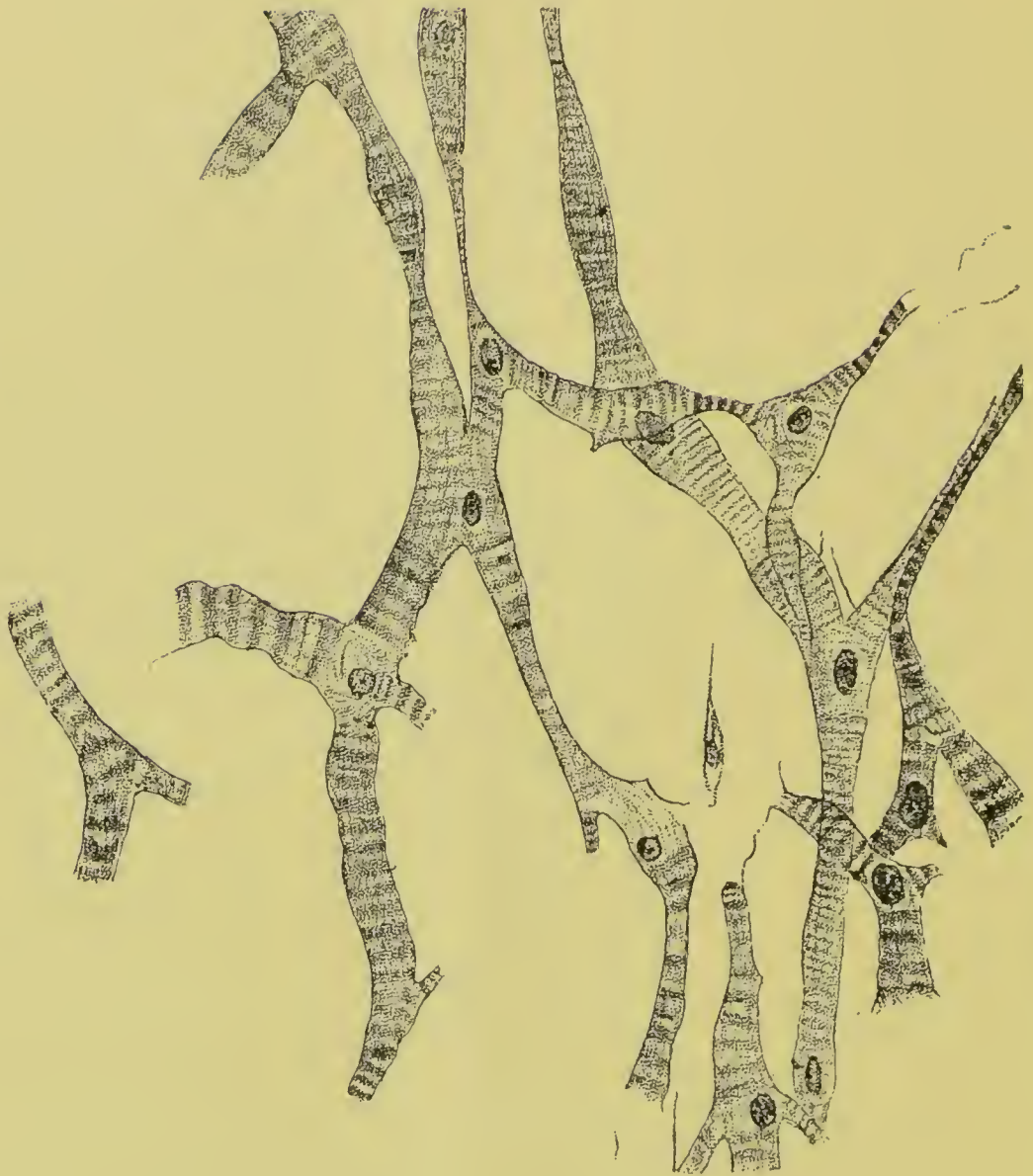


FIG. 2.

A small portion of Plate XII., Fig. 4, drawn under the one-twelfth oil immersion, to show the character of the muscular fibres lying in the fibrous tissue. They are seen to be sometimes fusiform, sometimes much branched cells, the branches being either comparatively thick or tapering off to very fine threads, which again become larger, again branch, and are connected into a network with the branches of other similar cells. The nucleus usually causes a bulging of the cell. Transverse striation is usually very well marked.

*Experiments on the living heart.*

Just as in the histological examination, so in the experimental my first observations were made on the hearts of young animals and, as was to be expected, a very close relation between structure and function was soon found to exist.

In the first place it seemed reasonable to suppose that if the heart is to be regarded as an organ with complete muscular continuity of all its parts, an artificially excited wave of contraction would be able to pass over its substance not only in the direction taken by the normally occurring contraction from auricle to ventricle, but also in the reverse direction from ventricle to auricle. Such a mode of contraction has been described by MacWilliam as the result of a single mechanical stimulus, or of the local application of heat, to the apex of the ventricles in the intact normally-beating vigorous heart.

In newly-born animals, in which the heart remains excitable for a considerable time after the death of the animal, I have found that such a mode of contraction may be induced with great ease, either by applying induction shocks to the apex of the ventricle at a rate slightly faster than the normal beat of the heart, or by passing induction shocks at any desired rate into the ventricle of a heart inhibited by vagus stimulation. It must be stated, however, that vagus stimulation was found to admit of the reversed beat being brought about only if just the right strength of current was used, and I have often found that after the vagus had been severely excited it was quite impossible to produce the reversed rhythm until the heart had to some extent recovered from the inhibitory effect.

On the other hand, I have not observed the phenomenon described by some authors, of vagus stimulation being ineffective upon the hearts of newly-born animals.

By adopting a similar method I have been able to produce in the hearts of adult animals a similar reversal of the normal beat, and this fact by itself appears to me to be a very strong argument for the purely muscular nature of the conduction of the wave of contraction across the auriculo-ventricular groove. For supposing that such transmission were due to nervous agency, it would be easy to understand how the impulses could pass along the nerve trunks in a direction opposite to the normal, but it is difficult to conceive of end organs which, whilst normally acting in one direction only, should be ready at any moment to act in a reversed direction and to so change their functions that

from receiving stations they should become transmitting stations, and from transmitting they should become receiving.

And in order to throw more light upon this subject I have made some experiments which appear to me to give results which afford still stronger arguments against the nervous nature of the transmitting apparatus.

The experiments were undertaken with the view of determining the time relations of the excitatory process passing over the auriculo-ventricular junction, as it appeared that in the event of the wave of contraction taking the same period of time to travel from ventricle to auricle as in the reverse direction from auricle to ventricle a further proof of the muscular nature of the path would be established.

And the result of numerous experiments has been to prove that whilst in certain cases an appreciable difference in the times has occurred, yet as a rule no such difference exists, and the time taken by the contraction in passing over the groove on one direction is sensibly the same as that taken in passing in the other direction. So that in this case also the evidence appears to point to a muscular, as distinguished from a nervous, means of transmission. And more weight should perhaps be attached to these experiments from the following considerations.

In the case of newly-born animals we have seen that as a rule a more perfect muscular connection between auricle and ventricle exists than is the case in the adult, and in accordance with this peculiarity of structure I have found that the time taken by the wave of contraction to pass over the auriculo-ventricular junction is less in the case of young animals than in the case of adults, thus indicating that in the former the short time taken is due to the perfection of the muscular connection and similarly the longer time taken in the latter is due to a less perfect connection. If then the perfection or otherwise of the muscular connection influences the time of transmission it is reasonable to suppose that the impulse is transmitted by the muscular tissue.

Another observation that seems to afford an argument for the muscular nature of the path of transmission is the following.

It is well known that in young animals the heart continues to beat for a considerable time after the death of the body, whilst in the case of adult animals under similar circumstances the heart ceases to beat almost immediately. In the latter case however although the whole heart does not beat and therefore one is apt to suppose that it has lost its automatism, yet close observation shows that the right auricle is



still active, and indeed may continue so for a considerable time. Is it not possible then that in the young animal the heart as a whole continues to beat because the contractions initiated at the venous end are able (in consequence of the very perfect muscular connection) to pass to the other parts of the heart whilst in the case of the adult the less perfect connection forms a block past which the contractions are unable to go?

In the same way it may be possible to explain the pause which occurs between the contraction of auricle and ventricle as the result of the differentiation of the muscular tissue of the heart at the groove. It has been seen that in the newly-born animal a large number of undifferentiated fibres pass from auricle to ventricle and in accordance with this peculiarity of structure it has been seen that the time taken by the contraction to pass the groove in these animals is short. In older animals in which the number of fibres is less and in which the differentiation has taken place the time is longer; in adult animals a very pronounced modification of the form and arrangement of the muscular fibres found at the auriculo-ventricular junction has been seen to occur. It seems then not impossible that the object of the modification of the muscular elements at the junction of auricle and ventricle may be to delay the passage of the wave of contraction, which quite conceivably may meet with considerable resistance when it leaves the thick muscular fibres of the auricle and passes into the network of fine fibres described as occurring between these and the ventricular muscle. For any variation of structure naturally leads to a variation in function, such variation of function having a definite ratio (in respect of magnitude and direction) to the variation of structure. And it has been shown that the variation in structure of the muscular fibres at the groove is in the direction of non-striped muscle, and accordingly a variation of function also in the direction of non-striped muscle might reasonably be looked for. Such a variation would cause the tissue to conduct less rapidly, and slowness of conduction has been shown to be a characteristic of the muscular tissue in this situation.

And Marchand's contention, that the time which elapses between the excitation of the auricle and contraction of the ventricle is too long to be regarded as being occupied in the transmission of a wave of contraction along such a tissue as that formed by the muscular fibres of the ventricle, loses its weight; since we know that a bridge of tissue of far less conducting power is interposed in the path of the contraction and accounts for a large part of the time occupied.



Moreover Gaskell has shown that in the heart of the tortoise after section of all nerves passing from sinus to ventricle a bridge of auricular muscle may be left over which the contractions pass without any modification. By gradually narrowing this bridge however an artificial block (complete or partial) may be introduced into the path of the contraction, and under these conditions it is apparent that a wave of contraction passes from the sinus up that part of the auricle in connection with it as far as the bridge, and then after a slight pause down the part of the auricle in connection with the ventricle to the sulcus, where another pause occurs, and then the ventricle contracts. If the bridge of tissue is still further reduced it is seen that every contraction is not able to pass, but that every second contraction passes over and when it reaches the ventricle induces a ventricular contraction.

That is to say, by lessening the cross section of the muscular path over which the contraction has to travel we are able to imitate the natural pause which normally occurs at the auriculo-ventricular groove. And further than this, when the vitality of the heart is declining and the conductive power of the tissue at the groove is presumably less than normal, a condition is very often seen in which not every, but every second contraction of the auricle is able to induce a contraction of the ventricle; this corresponds with the condition described by Gaskell in the tortoise heart, in which the bridge of tissue was made so narrow that a similar block of every second contraction took place. In the one case the bridge is naturally somewhat narrow and a slight artificial diminution of conducting power is sufficient to interrupt every other contraction, in the other case the conductivity is naturally good and the artificial narrowing has to be pushed to an extreme to produce a similar effect. In both cases however the phenomena are similar.

It has also been shown by Gaskell that in the case of the frog a similar block may be produced by a gradually increasing compression of the tissues at the auriculo-ventricular groove, and by a specially constructed clamp he has been able to so apply the pressure to the excitable structures as to obtain results almost identical with those described above as the result of section in the tortoise heart.

In the case of the Mammalian heart almost precisely similar results may be obtained by the use of a suitably constructed clamp, and using such an instrument I have been able to verify for the Mammal almost all the effects described by Gaskell as obtained in the frog.

It is thus seen that just as in the frog and tortoise so also in the

mammal an interruption, partial or complete, of the wave of contraction can be produced by artificial means, the necessary conditions being that the cross section, or the conductivity, or both, of the cardiac tissue forming the path of the contraction wave should be reduced.

And by these means it is possible to arrange a condition of things in which the pause artificially produced presents characters almost indistinguishable from those of the pause normally taking place at the auriculo-ventricular groove. And the question irresistibly presents itself, Is not the pause naturally produced due to similar causes as the pause artificially produced? It has already been shown that the cross section of the muscular tissue at the groove is reduced (and it has been proved by Romanes in the case of *Medusæ* that the rapidity of conduction varies directly as the sectional area of the conducting path) and it has been shown that its conductivity is diminished. Moreover it has been shown that these are the conditions necessary to produce an interruption of the contraction wave. It seems then impossible to come to any other conclusion than that the pause normally occurring at the auriculo-ventricular groove is due to the passage of the contraction wave over a muscular tract of reduced cross section and diminished conductivity.

#### *Conclusion.*

The conception of the structure of the mammalian heart put forward in this paper will necessitate a complete revision of our views of the mode of action of that organ so far as the transmission of the contraction over the auriculo-ventricular junction is concerned. For whereas in the past it has been supposed that the mammalian heart differed from the heart of cold-blooded animals in having a complete break of muscular continuity between auricles and ventricles, it has now been shown that no such break exists, but that the auricles are connected with the ventricles both by strands of altered muscular tissue (specially well developed in the lower mammals) and by a more complex system of branching and anastomosing fibres which penetrate the fibrous tissue between the two chambers (specially well developed in the higher mammals).

Muscular continuity being established and a variety of observations on the living heart, such as the study of the reversed beat, the time relations of the reversed as compared with the direct beat, the time relations of the beat in animals of different ages, the effects of compression on the auriculo-ventricular groove, and the study of the beat



in the dying heart, all tending towards an explanation of the transmission of the contraction from auricle to ventricle as a case of simple muscular conduction, the ideas that have been held as to the nervous nature of the transmitting apparatus become less necessary than up to the present time they have been. The results of observations on the hearts of cold-blooded animals in which the muscular connection has long been known to exist become to a certain extent applicable to the heart of the mammal, and as has been seen, many of the effects obtained by artificial interference with the muscular structures existing at the groove in cold-blooded animals may be obtained with almost equal ease in the case of the mammal. The passage of a contraction over the auricular wall also has been proved to occur independently of the larger nerves, inasmuch as the contraction can pass over a zigzag strip of tissue made by a series of interdigitating incisions carried in any direction, and the free application of ammonia to all visible nerves does not arrest the contraction either in auricles or ventricles. The passage of the contraction over the cardiac tissue of the heart then appears to occur as a simple muscular wave, and the transmission of the contraction across the auriculo-ventricular groove appears to be of a similar nature.

In a later paper I propose to deal with the exact localisation of the muscular connection between auricles and ventricles, and to describe the result of further experiments upon the functions of the mammalian heart.

### *Methods.*

The method of staining that was found to give the best result was as follows:—the sections were lightly stained in picrocarmine, washed in water, dehydrated with alcohol saturated with picric acid, cleared in oil of cloves, and mounted in xylol balsam. By this method the connective tissue was stained red, the muscular fibres a very characteristic brownish yellow, and the whole section was rendered so transparent that it was possible to follow individual fibres to a much greater distance than could have been done in glycerin or Farrant preparations. For studying some special points, however, such as the branched fibres to be described later, it was found best to make use of preparations stained with picrocarmine and mounted in Farrant's medium.

The photographs were made with the lenses *AA*, *BB*, etc. of Zeiss, with the homogeneous immersion system of one-twelfth in. focus, and the apochromatic objectives of 16 mm. and 4 mm. focus. The projection

eyepiece No. 2 was used and all the photographs were taken by the arrangement of apparatus made use of in the Physiological Laboratory at Oxford. The drawings have been made by the aid of the new form of Abbe's camera as manufactured by Zeiss, and the lenses used have been those mentioned above.

The graphic records have been made by means of a specially devised form of recording apparatus consisting of a glass plate fixed in a brass frame which can be moved at any desired speed by water pressure. The levers used were also specially devised to avoid "loss of time" and also to work with as little friction as possible whilst still giving a very perfect trace.

The exciter used was a Bernstein's differential rheotome, the galvanometer blocks being thrown out of gear and the exciting contact alone used.

For the use of this apparatus my best thanks are due to Prof Burdon Sanderson, who has also given me much valuable advice during the course of the investigation.

I wish also to record my indebtedness to Prof. Gotch, who has given me many useful suggestions.

#### EXPLANATION OF PLATE XII.

Fig. 1. A photograph of a section of the heart of a young Rat, showing junction of left auricle and left ventricle. The auriculo-ventricular valve is to the left. It is seen that the muscle fibres of the auricle are continuous with those of the ventricle on the one hand, and with those of the valve on the other. Stained carmine.

Fig. 2. Photograph of section of the heart of adult Rat. Shows junction between left auricle and left ventricle. The lower mass of muscular tissue is a part of the wall of the left ventricle, and at the upper part of the figure and to the left is a part of the left auricle. There is no interruption of muscular continuity. Above and to the right is a blood-clot in the auricular cavity. Stained logwood.

Fig. 3. Photograph of a section of heart of adult Rat, showing junction between auricle and ventricle. The auriculo-ventricular valve is to the right of the figure.

Fig. 4. Photograph of fibrous tissue at auriculo-ventricular groove in heart of Monkey. Shows the branched and very slender muscular fibres imbedded in the fibrous tissue, and their connection with the fibres of the ventricle. To the left of the figure the network is fairly dense, on the right the fibres are somewhat thicker. At the lower part of the figure the mode



of termination of the ventricular fibres is well seen. A process-block of a drawing of this section has been printed with the text.

Fig. 5. Photograph of auriculo-ventricular groove in heart of Monkey. This figure shows the way in which the auricular fibres branch on reaching the fibrous tissue. At the lower part of the figure on the right a stellate mass of auricular muscle is seen, some of the fibres of which become continuous with some of the scattered branched muscle cells lying in the fibrous tissue. At the top of the figure the tapering terminations of the ventricular bundles are seen, and on the right a few of the branched fibres lying in the fibrous tissue.

Fig. 6. Photograph of auriculo-ventricular groove in heart of Monkey. Shows the way in which the auricular muscular tissue becomes broken up into stellate masses as it approaches the fibrous tissue, and the manner in which these stellate masses become connected with one another by lateral branches. To the right of the figure a few branched cells are seen.

*Reference Letters.*

<i>A.</i> Auricle.	<i>L. V.</i> Left Ventricle.
<i>V.</i> Ventricle.	<i>Val.</i> Valve.
<i>L. A.</i> Left Auricle.	<i>F. T.</i> Fibrous Tissue.

Oxford, March 1892.

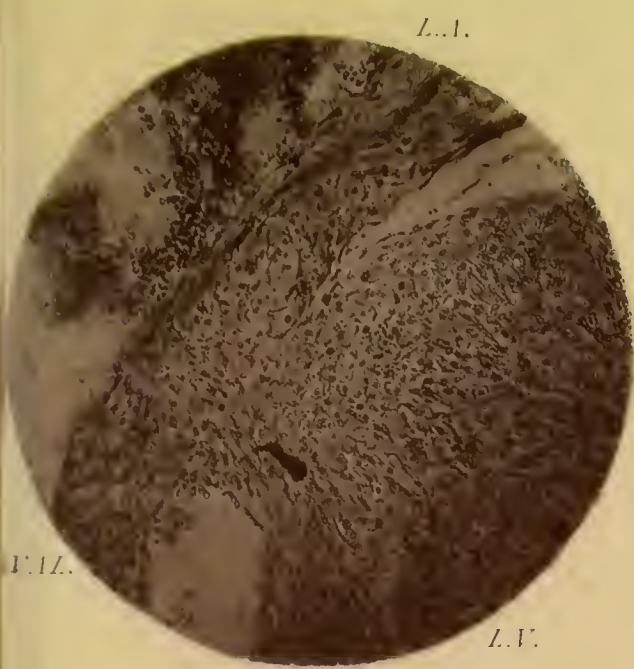


Fig. 1.

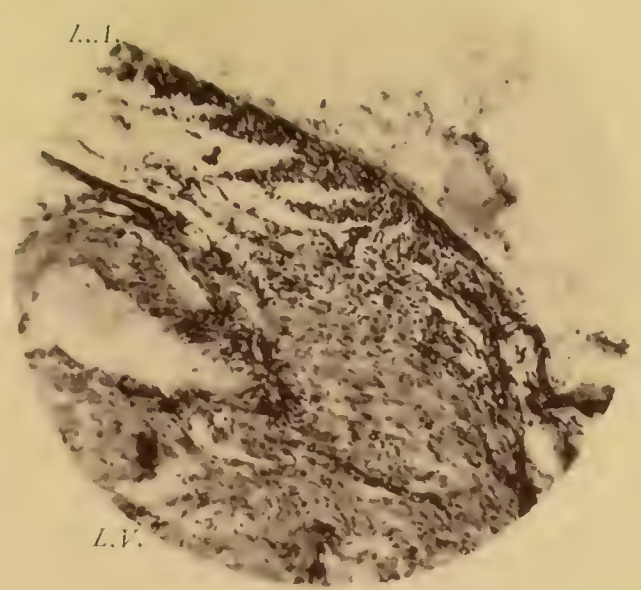


Fig. 2.

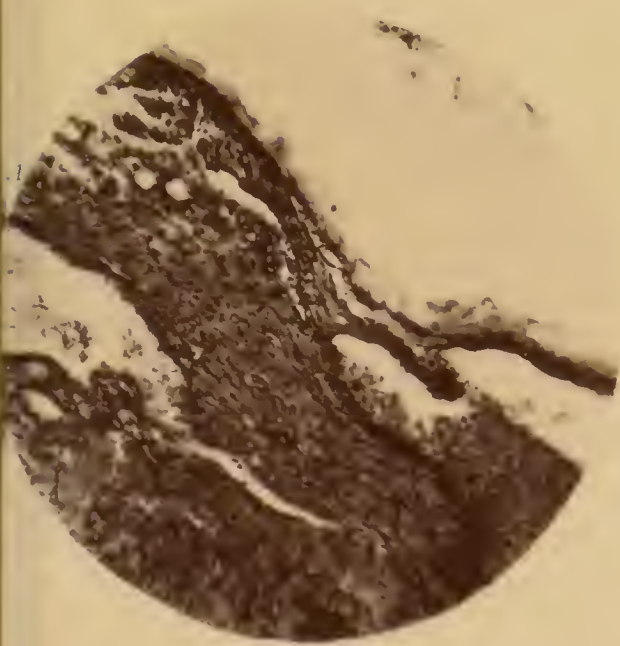


Fig. 3.

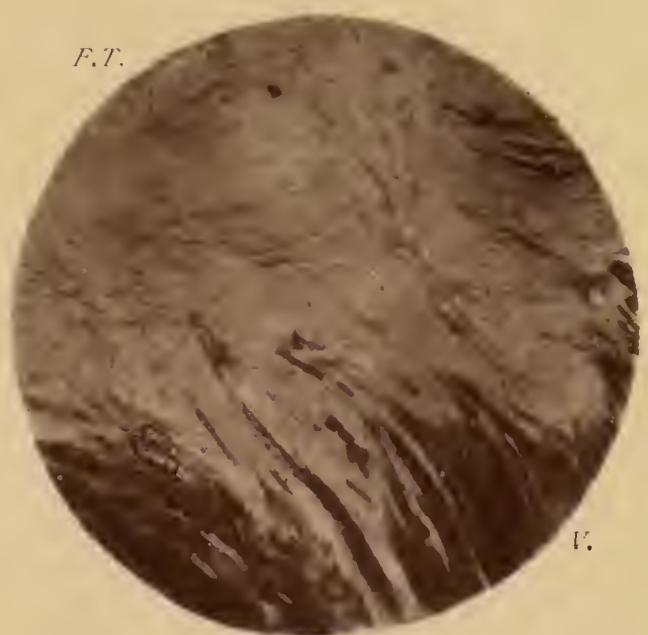


Fig. 4.

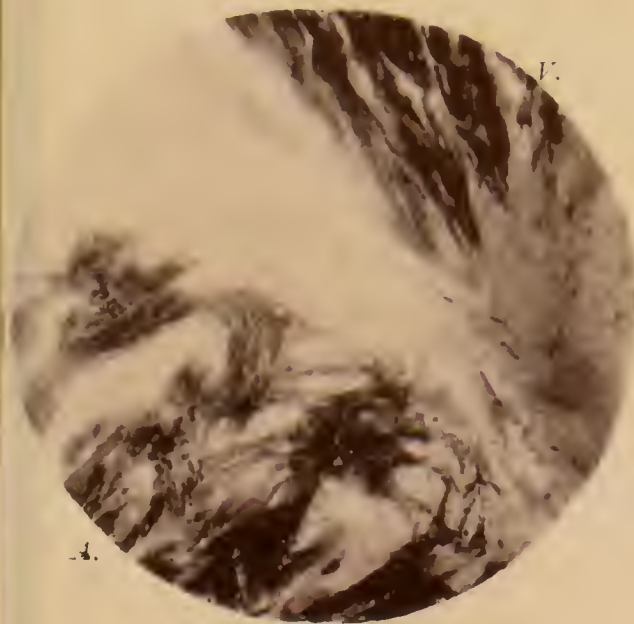


Fig. 5.

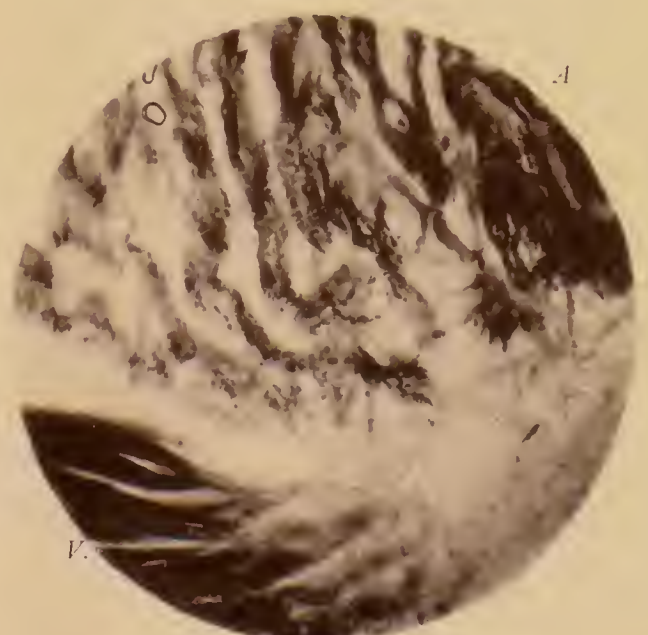


Fig. 6.







